

INTRODUCTION

The recent impacts of climate change have threatened the health and functioning of forested ecosystems on a global scale. Due to the shifting global climate, the frequency and severity of disturbances are increasing, inevitably causing an increase in disturbances overlapping in time and space (Abatzoglou and Williams 2016, Hart and others 2014, Schoennagel and others 2017). Widespread tree mortality from altered disturbance regimes creates significant uncertainty about stand dynamics and recovery in many systems. Bark beetle epidemics and wildfires have historically shaped the disturbance regimes of western North American forests. The interactive effects of multiple disturbances are often inadequately studied, especially in high-elevation, often difficult to access forests, such as those dominated by Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*); understanding these interactions is imperative to the management and health of forested ecosystems. This study focuses on the effects of epidemic spruce beetle (*Dendroctonus rufipennis*) outbreaks, high-severity fires, and the subsequent species and structural diversity of subalpine forest regeneration and structure in northern Colorado and southern Wyoming.

This project collected data across 80 sites (fig. 11.1) to address three main objectives: (1) quantify fuels structure and regeneration across a chronosequence of spruce beetle outbreaks in addition to areas impacted by outbreaks and wildfires, (2) age seedlings to understand tree regeneration and recruitment in relation to the disturbances and long-term climate, and (3)

quantify fuels after spruce beetle disturbance for better assessment of fuel complexity in the event of wildfires.

METHODS AND RESULTS

To address objective 1, we collected fuels, stand structure, and tree regeneration data and modeled our plot design after Ott and others (2018), establishing 0.08-ha circular fixed area plots. Full methods can be found in Schapira and others (2021a). Analyses indicated a significant increase in fuel loading over time since outbreak, as aerial fuels were transferred to the forest floor following high tree mortality (fig. 11.2A). Tree seedling densities among outbreak and control sites differed significantly from burned areas, indicating that wildfires overrode the effects of spruce beetle disturbances on regeneration (fig. 11.2B). There was consistent Engelmann spruce seedling survival following beetle outbreaks, providing evidence for stable forest recovery following a single disturbance. We did not observe any life cycle changes in beetle phenology though we focused primarily on forest structural characteristics. However, fire was a dominant force in determining post-disturbance species composition, indicating continued prevalence of high-severity fire may prove detrimental for the persistence of spruce-fir species, while promoting shifts toward more drought- and fire-tolerant tree species (e.g., lodgepole pine [*Pinus contorta*]).

To address objective 2, we destructively sampled and aged 229 Engelmann spruce and subalpine fir seedlings on 30 of these original 80 sites. Here, we aged seedlings to understand age structure of understory trees within spruce beetle- and

CHAPTER 11

Effects of Spruce Beetle (*Dendroctonus rufipennis*) Outbreaks on Rocky Mountain Spruce-Fir Stand Characteristics

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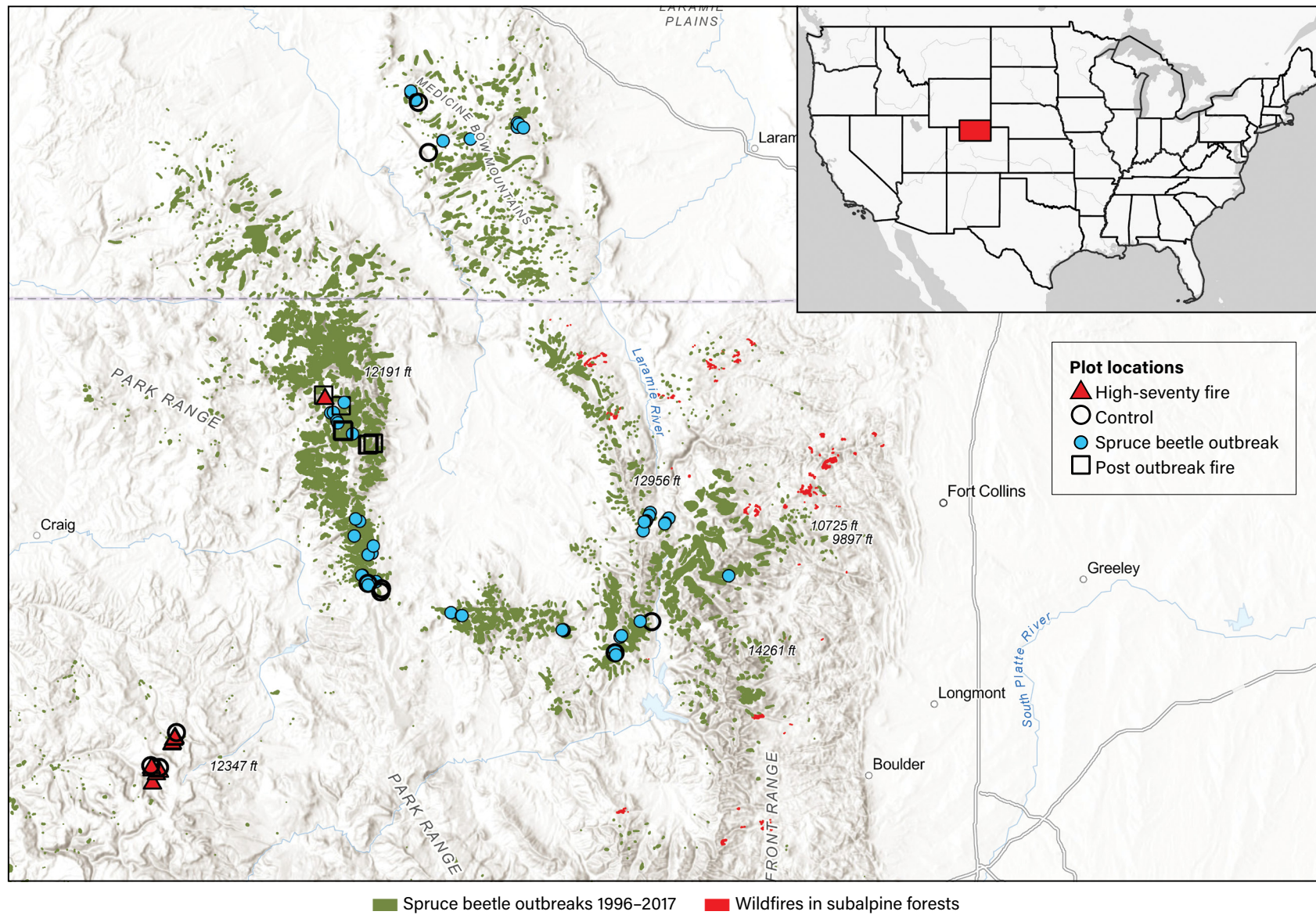


Figure 11.1—Study sites located in southern Wyoming and northern Colorado, across a chronosequence of spruce beetle outbreaks and area impacted by spruce beetle outbreaks and wildfires.

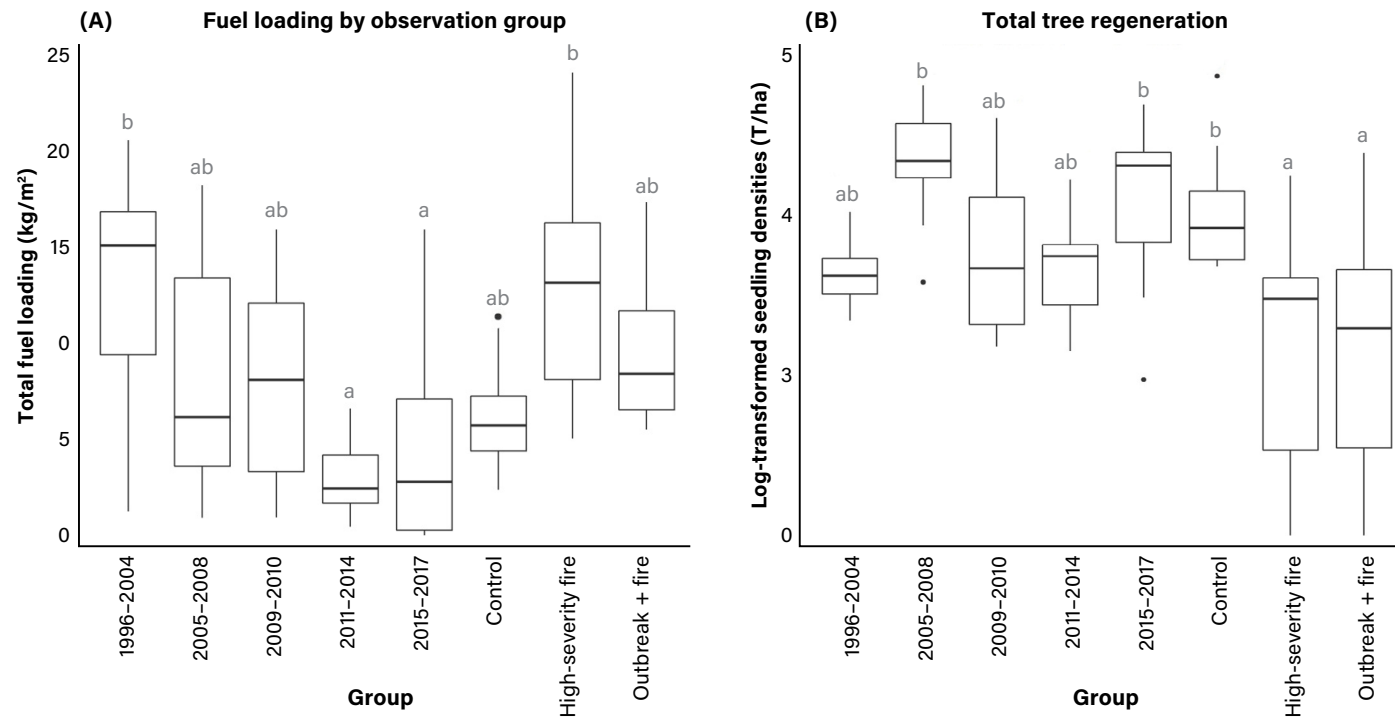


Figure 11.2—(A) Boxplots of total fuel loading by group; (B) boxplots of total tree seedling densities (all species) in each disturbance group. Bark beetle disturbances were pinned by year since outbreak, control sites were those with endemic levels of bark beetle activity and wildfire sites burned in 2002 and 2005, and “outbreak and fire” sites experienced a bark beetle outbreak prior to wildfires of these same years. Horizontal bars represent mean fuel loading of each disturbance group; height of boxes represents spread of 75 percent of data. Different letters indicate statistically significant differences between groups from a Tukey’s honestly statistical difference (HSD) analysis. As shown on (B), analyses were conducted on log-transformed seedling densities; raw densities are graphically displayed. Units are in log transformed trees per hectare.

wildfire-affected stands. Full methods can be found in Schapira and others (2021b). We compared climatic conditions between years with high tree seedling establishment and nonestablishment years to ascertain regional drivers of tree seedling recruitment in subalpine forest. Both height and terminal bud scar counts were significant predictors of seedling age, although correlations were weaker in older seedlings that exhibited suppressed growth (tables 11.1 and 11.2). Growing season precipitation had a significant positive relationship with spruce-fir establishment, while minimum temperatures, annual vapor pressure, and climatic water deficits had significant negative correlations with subalpine tree establishment. Height and terminal bud scar counts did not accurately predict precise ages of subalpine tree establishment from beetle-affected stands but provided more accuracy in post-fire tree establishment. Average climate conditions compared to long-term climate may provide suitable conditions for low levels of tree establishment in spruce-fir stands. However, large spruce-fir establishment pulses occurred in cooler and wetter growing years compared to the long-term average.

To address objective 3, we created a post-outbreak fuels photo series and modeled it after the natural fuels photo series, which includes six volumes that represent different forest types across the United States (Ottmar and others 2000). This post-outbreak fuels photo series represents spruce-fir forests in different stages of spruce beetle outbreak recovery and spruce-fir stands unaffected by spruce beetles for comparison. This project was published through the Southern Rockies Fire Science Network (Schapira and others 2021c).

Table 11.1—Generalized linear models for predicting Engelmann spruce seedlings ($R^2 = 0.8158$)

Engelmann spruce	Estimate	Standard error	t-value	p-value ^a
(intercept)	-6.62	2.36	-2.81	<i>0.006</i>
Height (cm)	0.19	0.05	3.96	<i>0.0001</i>
Bud scar count	1.42	0.13	11.00	<i><0.0001</i>
Disturbance type: burn ^b	-6.24	2.70	-2.31	<i>0.023</i>

^a Significance indicated in italics, and *p*-values indicate significance of predictor variables on Engelmann spruce age.

^b Outbreak sites are the baseline category for “disturbance type.”

Table 11.2—Generalized linear models for predicting subalpine fir seedlings ($R^2 = 0.7992$)

Subalpine fir	Estimate	Standard error	t-value	p-value ^a
(intercept)	-4.69	2.34	-2.00	<i>0.048</i>
Height (cm)	0.095	0.04	2.41	<i>0.018</i>
Bud scar count	1.45	0.12	12.49	<i><0.0001</i>
Disturbance type: burn ^b	-7.49	2.94	-2.55	<i>0.012</i>

^a Significance indicated in italics, and *p*-values indicate significance of predictor variables on subalpine fir age.

^b Outbreak sites are the baseline category for “disturbance type.”

DISCUSSION AND CONCLUSIONS

This study demonstrates that subalpine forests are impacted differently by different disturbances. Tree regeneration was abundant following spruce beetle outbreak, but post-fire seedlings were less common and were predominantly lodgepole pine and aspen (*Populus* spp.), rather than Engelmann spruce and subalpine fir that previously dominated these landscapes. However, unlike concerns at lower elevation forests (Chambers and others 2016), all plots had tree seedlings. Climate change will likely continue to play a role in tree establishment in both burned and bark beetle-affected stands, and this pattern is likely more pronounced in burned sites due to the lack of canopy cover and favorable microsite conditions. Tree regeneration and forest recovery in these long-lived systems may take many decades or even centuries to recover to a similar species dominance, and these processes may be driven by current and future climate. In spruce beetle outbreak sites, tree regeneration was abundant and high fuels loads were common, especially at longer times since outbreak. Small trees do not necessarily equate to young trees, especially in these dense forests that are dominated by shade-tolerant species (Hankin and others 2018, Veblen 1986). We found tree seedlings on all 80 study sites; however, spruce beetle outbreak sites had a larger proportion of subalpine fir and, in some cases, thousand seedlings per hectare, and we may see a change in dominance as others have hypothesized and observed (DeRose and Long 2010, Schmid and Frye 1977). Burned sites had tree regeneration dominated by lodgepole pine and aspen, indicating at least short-term conversions in forest dominance, as others have found in

fire-affected stands (Harvey and others 2014), but this may create conditions conducive in the years to come for Engelmann spruce and subalpine fir regeneration as they are more shade tolerant. Given the projections for both more wildfires and hotter and drier climatic conditions (Higuera and others 2021), the future of these forests is uncertain and continued monitoring of these complex forests at the top of the world is important to consider.

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